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On the transpiration of Fouquieria splendens*

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The present paper is an account of one of several studies which were carried on in 1904 by the polymeter method upon plants in place. It will not be necessary to give here a description of the method, since this will soon be done elsewhere,† but a certain peculiarity attending its use may be briefly referred to. By the new hygrometric method it is possible to study the transpiration of a plant in the field not only once, but many times, without injury to it. The fact that repeated observations of transpiration can be made rendered it possible to learn not only the daily but the seasonal rate as well. Thus a transpiration history, not indeed without many gaps, has been traced. The experiments were begun in February and were continued from time to time until after the rains of summer were over.

In addition to the transpiration observations, and in connection with them, certain environmental factors were observed and measured and a comparison was made between them and the rate of transpiration. This part of the work was from necessity secondary, but despite this enough was done to establish certain important facts and to indicate lines of study which may be profitably followed in the future.

The difficulty in tracing the influence of external conditions on the rate lies, among other things, in the changeableness of these

* Papers from the Desert Botanical Laboratory of the Carnegie Institution, No. 10.

† Cannon, W. A. A new method of measuring the transpiration of plants in place. Annals of Botany, *ined.*

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factors from day to day. For outdoor work, therefore, where the conditions cannot be controlled beyond a certain limit, it is a great advantage when the climatic factors vary in a uniform manner, or when certain conditions are so pronounced that their influence is unmistakable.* The year 1904 was an especially fortunate one for field work because, as will be shown below, uniform variations in the temperature of the air, in humidity and in other climatic features were maintained for days together, and the uniformity of the environmental factors made the outdoor work similar in this regard to that done in the laboratory where the conditions of experiments are to a degree under control.

Apparently the main cause of the uniformity of the climate in 1904 was the small rainfall of the year. At the same time the most disturbing feature of the uniformity was the sudden and infrequent rains. Since the rain is an all-important factor in the biology of desert plants, it consequently happens that the history of their transpiration reflects most clearly the influence of rain and of drought, so that the relation of transpiration to these features constitutes the key-note of the studies. For this reason it is best before presenting an account of the experiments to give an outline record of the climate for the year, in which emphasis is placed on the humidity of the air and on the rainfall.

CLIMATE FOR 1904

The normal rainfall at Tucson, the average for 15 years, is 11.74 inches.* In 1904 the total precipitation was 7.79,† or about 75 per cent. normal.

The distribution of the rains throughout the year, both the usual distribution and that for 1904, is shown in FIGURE 1. It will be observed from the figure that the winter rains of the year were very light, but the summer rains, particularly those of August, were slightly greater than usual. This distribution operated therefore to intensify the dryness of that portion of the year when the plants are naturally least active, and at the same time to bring about unusually favorable vegetative conditions at the season of the greatest activity, that is, in summer.

* Coville, F. V., & MacDougal, D. T. Desert Botanical Laboratory of the Carnegie Institution, 26. 1903.

† From data provided by the University of Arizona.

The significance of the small rainfall of the year is a factor which must be taken into account, and, although it seems difficult to express this concretely, it may be better appreciated if we consider the relation of the precipitation of the year to the possible total evaporation. The normal annual evaporation at Tucson is estimated to be 90 inches.* The ratio between the normal annual rainfall and the evaporation is therefore 1 : 7.7. If we suppose for the moment that the decrease in 1904 of approximately 25

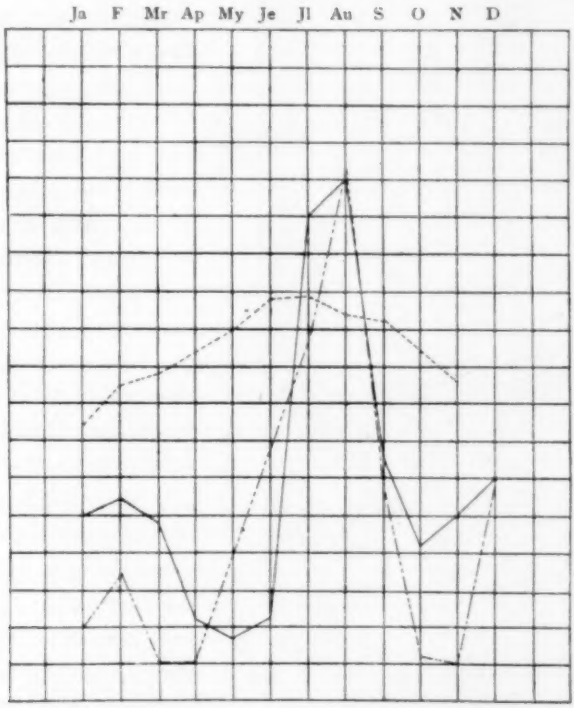

FIGURE 1. The rainfall and the mean maximum temperature at Tucson. The normal rainfall is represented by a solid line; the rainfall in 1904 by a broken one (- - — - -); 5 mm. = one-half inch precipitation. The mean maximum temperature for the year is given by the second broken line (- - - - -); 5 mm. = 10 degrees Fahrenheit.

per cent. in the precipitation was accompanied by a proportional increase in the evaporation for the year, the ratio would be greatly altered. An increase of 25 per cent. in the total evaporation would make 112.5 inches; and the ratio between precipitation and evaporation becomes 1 : 12.7.

* Coville & MacDougal, *l. c.* 27.

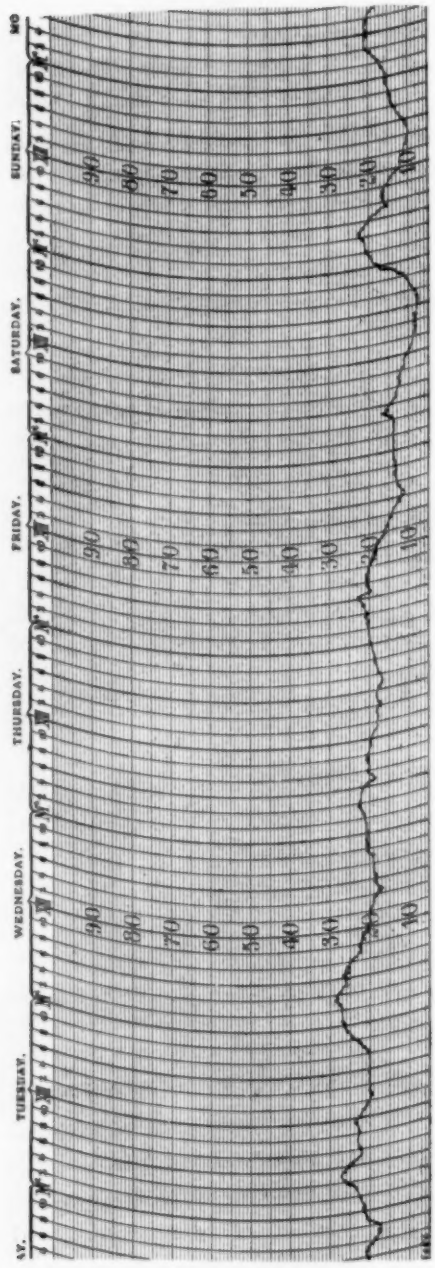

FIGURE 2. Hygrographic record for the week ending July 4.

Whether the amount of evaporation for 1904 and the relation of that amount to the rainfall of the year as given are exact expressions of the true ratio and of the actual amount does not matter for the present—the striking fact, which is inadequately shown by the illustration, is that a really small decrease in the annual rainfall may be a most important fact in the nicely balanced life relations of desert plants.

A climatic condition, the relative humidity, which is closely associated with the rainfall and thus with the rate of transpiration, may be passed over in few words. As the seasonal rainfall was less than usual, so also the average relative humidity was probably correspondingly lower. What the departure from the normal may have been, however, I have no observations at hand to show. Certain it is that the humidity at times was very low, as for instance during the entire week ending July 4 it did not even

at night-time exceed 28 per cent. In the daytime it was always low (FIGURE 2).

A certain peculiarity of the changes in the relative humidity, which may have to be taken into account when the biological significance of the absorption of water by the aerial parts is considered, may be pointed out. I refer to the fall of the humidity which ordinarily occurs soon after a storm has passed. This is illustrated in FIGURE 3. On Wednesday night, Thursday and Thursday night a small rainfall (.04 in.) occurred. During the rain the humidity was rather high even in the laboratory where the hygrograph was placed, but within twelve hours after it ceased the humidity was nearly as low again as previous to the storm.

The humidity remains high, however, for several days following a long storm, and since the most rain ordinarily falls in summer this peculiarity cannot fail to be of great importance to the desert plants.

As regards the temperature it will not be necessary for the present purpose to go into this phase of the climate of the year more than to mention certain striking characteristics.

The annual as well as the daily range was relatively large. During the driest portion of the summer, in June, the maximum for the year, 107° F., was recorded. The temperatures were somewhat lower after the rains of summer had come. (See FIGURE 1, which shows the mean maximum temperature for 1904.) In the colder part of the year, December to March, the thermometer reached the freezing point or below each month, and in January a temperature of 15° F., which was the minimum for the year, was reported. The range of temperature for the year was therefore 92° F.

Fifty degrees Fahrenheit was the greatest daily range. This was recorded in April in the midst of a rainless period. In August, on the other hand, during the summer rains, a daily range of but 31° F. was noted — this was the least of the year.

FOUQUIERIA SPLENDENS

Fouquieria splendens, "ocotillo" of the native Mexicans, is one of the most striking desert shrubs. It is well adapted, not only in the mature condition but as a seedling as well, to endure

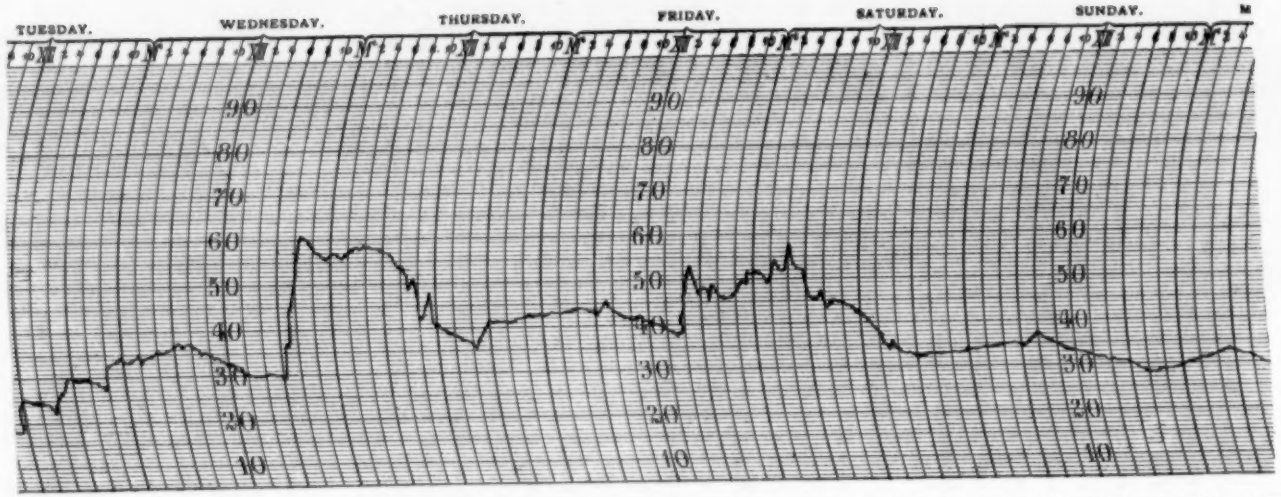

FIGURE 3. Hygrographic record for the week ending June 20. The figure shows a characteristic rise in humidity during a sudden storm and a characteristic fall after the storm has passed. In this instance the rain (.04 in.) occurred on Wednesday, at night, and on Thursday.

droughts apparently the most extreme, and it flourishes in habitats which are so dry as to be unfit for many desert plants.

A characteristic specimen of ocotillo is composed of a number (a dozen or more) of fairly straight branches, for the most part simple, which arise from the short main stem near the ground (FIGURE 4). The branches are from 2 to 5 meters in length, and bear spines which are regularly placed and which are morphologically midribs of the primary leaves.

During the dry seasons the branches are naked, but in the

FIGURE 4. *Fouquieria splendens* in leaf.

rainy ones they are well covered with rosettes of small leaves which are borne in the axils of the spines. The variation in the foliage is not a seasonal phenomenon but is directly associated with the distribution of the rainfall. Although seemingly lifeless during the droughts the plant is not dormant, since beneath its gray exterior there is chlorophyl-bearing tissue which enables the photosynthetic processes to go on, even if in a feeble manner, and consequently some transpiration may always be detected. When the rains return new leaves are formed with a promptness that is

surprising, and this phase of the plant's history constitutes one of the most admirable of adaptations to desert conditions.

RECORD OF EXPERIMENTS

All of the experiments on *Fouquieria* which are reported in this paper, but which constitute a part only of those performed, were conducted with the polymeter method of determining transpiration already mentioned,* and all were conducted upon plants or branches in place. It will only be necessary for the sake of clearness to point out the significance of the figures under the heading "Amount in milligrams." In each instance the first number refers to the amount of moisture present in the bell-glass, which encloses the plant, at the beginning of the experiment; the second number is the amount of moisture in the bell-glass at the end of the experiment. The difference between the two numbers constitutes of course the amount transpired in the time expressed in the first column.

TRANSPIRATION OF FOUQUIERIA NO. I. EXPERIMENTS 1–6

Fouquieria No. I is growing about 150 meters south of the laboratory building. It has half a dozen branches and is about one-half a meter high. The first three experiments were performed when the plant was leafless, because of the severe drought; leaves were present in the other experiments.

Experiment No. 1, February 12: Transpiration of leafless stems

The following data were derived from this experiment:

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
10:30	23.5	78° F.	65
12:30	27	81	68.5

Experiment No. 2, February 15: The same

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
11:40	28.5	77° F.	63.7
1:40	31	79	73.7

The rate of transpiration in Experiment No. 1 is 1.85 milligrams per hour; that in the succeeding experiment is 5 milligrams per hour.

* Cannon, *l. c.*

A slight rain, not enough to induce the formation of leaves, was recorded previous to the 12th. From subsequent experiments on the influence of the rains on transpiration it was observed that the rate may be increased without a change in the extent of the transpiring surface, and it is possible that the small but positive change in the rate which was recorded in Experiment No. 2 is directly traceable to the earlier rain.

In the experiments on the naked stems of *Fouquieria* it was suspected that the hygrometric method did not reveal the true condition of affairs inasmuch as it did not show how much of the moisture which had been evolved from the plant was subsequently absorbed by the dry branches. The affinity of air-dry stems of *Fouquieria* for atmospheric moisture had been demonstrated in the laboratory in the following manner: Leafless branches were removed from the plant, the cut end was coated with vaseline and the branch was placed in a beaker containing about two centimeters of water. The water very promptly ascended for several centimeters the surface layers of the branch, which also increased considerably in weight. The same behavior of leafless stems was also observed outdoors. In every instance the portion of the stem which had the affinity for water was the *younger* portion. Later the outer cortical part of the branches is infiltrated with a waxy substance which is impervious to water. To learn whether air-dry stems would absorb water-vapor also the succeeding experiment was devised.

Experiment No. 3, February 16: Absorption of hygroscopic moisture

The apparatus was set up in the same manner as if to determine the transpiration but with the addition of an arrangement by which air charged heavily with vapor was made to pass into the bell-glass. As soon as the humidity of the air of the bell was increased sufficiently, the openings into it were tightly closed and the reading of the polymeter was taken. The following is a brief of the experiment.

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
10:25	65	83° F.	176
11:15	53.5	88	168.7

In 50 minutes the stems absorbed 7.3 milligrams of moisture.

Although this experiment and others not reported indicate that under certain conditions leafless branches of *Fouquieria* can and in fact do absorb appreciable amounts of water and of water-vapor, they do not show that the water or the vapor is of physiological significance. Whether such is true I have not been able to demonstrate; since all the evidence thus far accumulated is negative.

Experiments 4–6: Effect of rains

The immediate effect of rains upon the rate of transpiration was repeatedly observed. When they resulted in an actual increase in the water-supply of the plant, the rate became greater, and later, as the available water-supply was decreased, the rate of transpiration became smaller. This was shown by the experiments on February 24 and March 4, 10, and 17, when leaves were developing, when they were mature, and when they may be termed senile. The rates for these experiments were respectively 47.5, 120, 24.4, and 13.7 milligrams per hour.

The intimate connection of the rate with the rains is also shown, and more strikingly, in the experiments which were performed soon after the rains of May. Between the experiments which were carried on during the latter part of March and those of May the plant was defoliated on account of the continuation of the drought. The rains of May were distributed as follows: May 10, .47 in.; May 11, .75 in. (the latter fell between 1:40 and 2:15 P.M.); May 12, .02 in. and May 16, .06 in. As a result of this sudden and considerable rainfall the mountain upon which the Desert Botanical Laboratory is situated, which had been very dry all winter, was thoroughly wet, and the mesa between it and the Santa Cruz River was covered with water. This rain had a very marked effect upon all vegetation. Trees and shrubs which had been without leaves all winter put out leaves promptly, the cacti which had become badly shriveled from loss of water directly became plump, but perhaps the most noticeable response was given by the fouquierias. Up to the time of this storm *Fouquieria* No. I and other ocotillos were leafless. On Friday, May 13, 48 hours after the heaviest fall of rain, *Fouquieria* No. I was rapidly coming into leaf, and by the afternoon of the following day these were of nearly mature size. The three succeeding experiments

were performed Friday, Saturday and Monday — May 13, 14, and 16 — and they illustrate how promptly the plant availed itself of the more favorable water-supply.

Experiment No. 4, May 13

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
2:55	33.5	93°F.	122.5
3:05	49	93	180

The rate is 345 milligrams per hour.

Experiment No. 5, May 14

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
9:48	30	91°F.	103.7
9:56	66.5	94	231.2

The rate is 956.2 milligrams per hour.

Experiment No. 6, May 16

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
9:15	25	92°F.	88.7
9:20	66.5	93	245

The rate is 1875.6 milligrams per hour.

Summary of experiments on Fouquieria No. 1

	Transpiration in milligrams per hour.
February 12 (without leaves)	1.8
" 15 "	5
" 24 (in leaf)	47.5
March 4 "	120
" 10 "	24.4
" 17 "	13.7
May 13 "	345
" 14 "	956.2
" 16 "	1875.6

TRANSPIRATION OF FOUQUIERIA NO. II. EXPERIMENTS 7–9

Fouquieria No. II, which is growing nearly north of the laboratory and a little lower on the mountain, is about the size of *Fouquieria* No. I. The character of the plant and the general nature of the habitat are indicated by FIGURES 5 and 6, and do not require further comment.

Experiment No. 7, March 22: Effects of irrigation

At this time the leaves of *Fouquieria* No. II, as of others on the mountain (see Effect of rains, page 406), had been nearly all discarded and most of those which remained were yellowish or

FIGURE 5. *Fouquieria* No. II, March 26.

partly withered and plainly indicated the harmful effects of the prolonged drought. The rate of transpiration was also very small, as the data of an experiment taken in the midst of the dry time shows.

The following data were derived from an experiment which was conducted before water was given the plant.

Time.	Per cent of saturation.	Tem rature.	Amount in milligrams.
1:30	55	80° F.	208.7
2:30	68	79	323.7

The rate of transpiration is .22 milligrams per minute for 100 sq. cm. of leaf surface, or 115 milligrams per hour for the entire plant.

FIGURE 6. *Fouquieria* No. II., April 8. This plant was without leaves, March 26 (*Figure 5*); it was given water March 26 and March 28 and was in leaf April 4.

Experiment No. 8, April 5: The same

To watch the reaction of the plant to an increase in the water-supply, at a time when it was suffering from an insufficient supply,

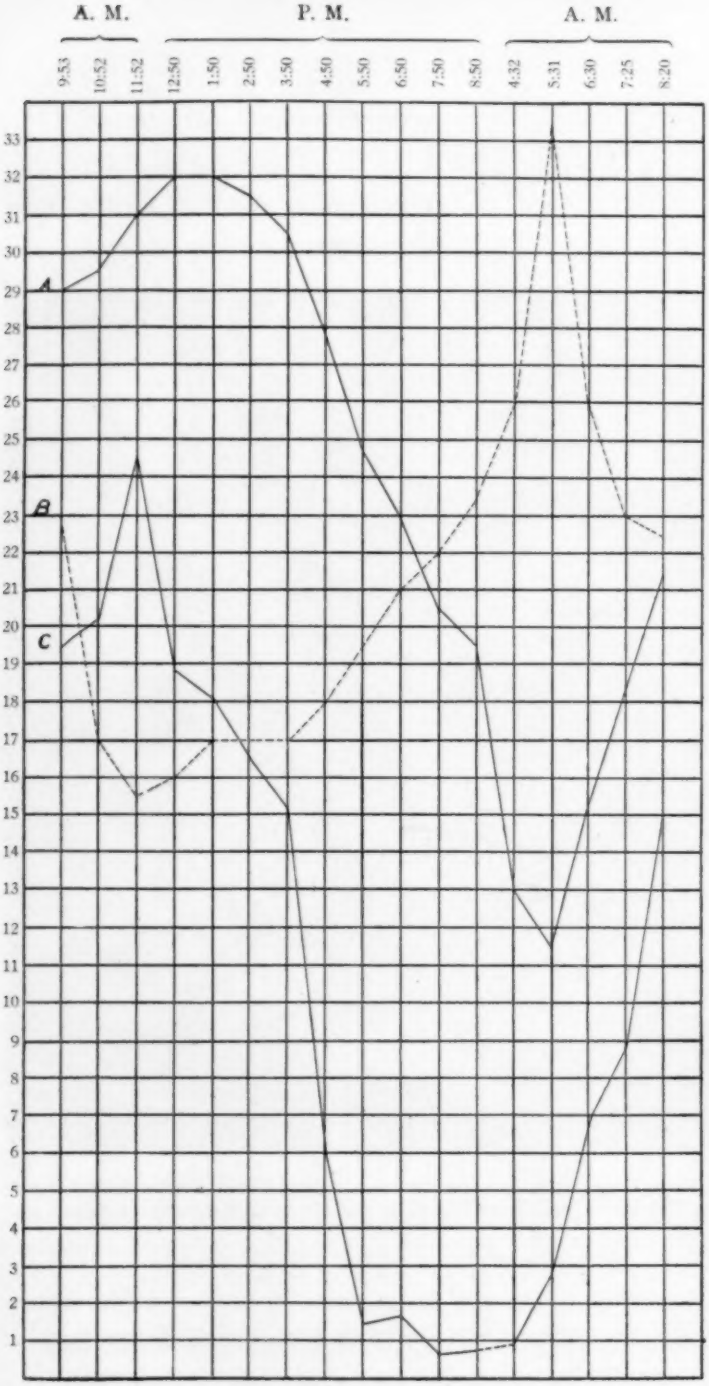

FIGURE 7. Daily periodicity in *Fouquieria*. *A* = temperature of air in degrees Centigrade. *B* = relative humidity, taken before each experiment. *C* = transpiration calculated to hourly periods, each space representing 100 milligrams. The time of each reading is given.

on March 26 and 28 about 20 gallons were put slowly on the ground at its base. As a result leaves were put out very promptly and the total transpiration was increased many fold.

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
10:03	28	26° C.	133.7
10:13	72	27	382.5

The rate of transpiration is 1492.8 milligrams per hour for the entire plant.

The history of the leaf-covering of *Fouquieria* No. II from February to August is of interest. The plant was seen to be in leaf the latter part of February, but as a result of the long drought in March the leaves fell away, so that the foliage which the plant formed the first part of April after it had been irrigated (Experiment No. 8) was the second leaf-covering of the year. April was a dry month and the plant was again defoliated. The drought was broken by a rain about the middle of May and *Fouquieria* No. II came into leaf for the third time. With the advent of dry and hot weather in June the leaves fell away again. On June 29 three gallons of water were poured slowly on the ground at the base of the plant. Leaf-buds were observed July 1, and at 2 P. M. on the succeeding day they were 1 cm. long. On the fifth the leaves were of mature size. (Compare FIGURE 6.) The leaves which were formed at this time, during an extremely dry season (FIGURE 2), soon withered and the plant was defoliated the fourth time. It is of interest to note that with the coming of the summer rains still another leaf-covering appeared on the plant, and therefore, it happened that *Fouquieria* No. II came into leaf five separate times between February and August, and that the exciting cause in each instance was an increase in the available water-supply.

Experiment No. 9, April 6 and 7: Daily periodicity

On the morning of April 6, at 9:53, the rate of transpiration of *Fouquieria* No. II was taken and it was observed at hourly intervals throughout the day until 8:52 P. M. The experiment was continued the following morning at 4:32 and readings were made every hour until 8:20 A. M. The record of transpiration was com-

plete for the daytime and for a portion of the night. A summary of the experiment is presented in FIGURE 7.

It will be noticed that the curve of transpiration reaches its highest point about noon and that in a general way it is similar to the curve expressing the temperature and that it opposes that representing the relative humidity. However, it neither closely follows the one nor flatly opposes the other. The maximum transpiration precedes the highest temperature of the day and a marked decline in the rate of transpiration takes place while the high temperature is maintained. The opposition of the curves representing the relative humidity and the transpiration is more consistent, but even in this case the afternoon decrease in the rate is more rapid than the rise in the relative humidity. It would be of much interest to compare the periodicity with the daily variation of other factors, as the temperature of the ground, and particularly the daily variation of the light, but unfortunately no data were available at the time to make this possible.

EXPERIMENT NO. 10, AUGUST 26: MAXIMUM RATE

As graphically shown in FIGURE 1, the heaviest rain of the year occurred in midsummer at a time when the temperature also was high. Although the rains did not extend over a period exceeding six weeks, the face of the desert was wholly changed because of them. Annuals in great variety and in large numbers appeared on previously barren stretches, and shrubs and trees which were apparently dormant during the droughts became covered with an abundance of large leaves. Thus the summer vegetation which appeared in consequence of the rains was tropical in its luxuriance. It was with much interest, therefore, that I observed the transpiration of plants at this period.

The following data were obtained about the close of the rainy period from the study of a branch in place:

Time.	Per cent. of saturation.	Temperature.	Amount in milligrams.
1:10 P. M.	33	98° F.	263.7
1:24	58.5	103	540

The rate of transpiration is 8.25 milligrams per minute for 100 sq. cm. of leaf surface. This is the highest rate observed for *Fouquieria* at any time during the year.

SUMMARY AND CONCLUSIONS

The leading points in this paper together with the conclusions may be briefly stated as follows:

1. The noteworthy feature of the climate of 1904 was the small precipitation, which was 75 per cent. normal. The rainfall was so distributed that little of it occurred in winter, spring or early summer, most of it coming in midsummer, Thus during most of the year the conditions of plant life were very severe; but in August especially they were favorable to plant growth.

2. The customary fleeting vegetation of late winter and of spring, composed mainly of annuals, did not appear, and the larger and long-lived forms either did not put on leaves at the time at all, or if they did so they were dropped when droughts returned. In summer, however, all vegetation was very luxuriant.

3. Although without leaves during periods of drouth *Fouquieria* nevertheless maintains at such times a feeble rate of transpiration.

4. Air-dry stems of *Fouquieria* in place can absorb hygroscopic moisture in appreciable amounts.

5. The rate of transpiration of *Fouquieria*, and of other shrubs, varied directly with the water-supply. The rate increased as an immediate effect of the rains and it decreased as the time past the rains became greater. Accompanying the increase in rate there was always an increase in the transpiring surface (although the rate may increase without the latter), but a decrease in the rate occurred without an immediate and corresponding decrease in the transpiring surface, although in the end this always became less.

6. The least rate of transpiration, when leaves were present, was observed during the dry and cool period the latter part of March. At this time a rate of .22 milligram per minute for 100 sq. cm. of leaf surface was recorded. The highest rate was observed August 26, near the close of the summer rains when the temperature was high. The August rate for the same time and area as in March was 8.25 milligrams.

7. A very striking adaptation to desert conditions is to be found in the promptness with which *Fouquieria* forms leaves when the water-supply of the plant is increased by the rains. As an example of this the following instances may be presented: For several weeks previous to the 11th of May one of the plants

studied had no leaves. Within 48 hours after the rain of May 11 it was well covered with them. On June 29, in the midst of a very dry period, three gallons of water were given to one specimen of *Fouquieria* and leaf-buds were observed on July 1, which by 2 P. M. on the succeeding day were 1 cm. long. On the fifth they were of mature size.

Fouquieria No. II formed five distinct leaf-coverings between February and August. The exciting cause in each instance was an increase in the water-supply. Very soon after the rains were over the leaves were dropped and excessive and destructive transpiration was thus avoided.

8. The daily periodicity of *Fouquieria* was observed in April. The rate varied in a manner corresponding to variations of the temperature, but not quite the same, and it inversely followed very closely the variation of the relative humidity.

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Studies on the effect of some concentrated solutions on the osmotic activity of plants*

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Turgidity, which is often of importance in bringing about rigidity in plant parts, is dependent to a great extent upon the osmotic pressure of the cell-sap, which keeps the cell-wall stretched to its greatest extent. The concentration of the cell-sap, upon which the osmotic pressure depends, varies according to the environment of the cell, and the permeability of the plasma-membranes.

Plasmolysis affords a means of studying the concentration of the cell-sap, and the changes which may be induced by the environment of the cell. If the cell lies in a solution more concentrated than the cell-sap, the greater osmotic pressure of the external solutes will cause a contraction of the protoplast. The protoplast will withdraw from the cell-wall to a greater or less extent, according to the increase or decrease of the difference between the external and internal osmotic pressures. It is this withdrawal of the protoplast from the cell-wall which constitutes plasmolysis.

In dealing with certain substances, glycerine, urea and acetamid, to which the plasma-membrane is more or less permeable, and which are considered harmless to the protoplast (Overton 17 and 18; Hampe 9; Beyer 2; de Vries 33; Klebs 10; Laurent 11; Meyer 14*b*), it was desired to ascertain if a stronger concentration of other substances would be necessary to bring about plasmolysis, after treatment with glycerine, urea, or acetamid, than under normal conditions.

METHODS AND EXPERIMENTS

In general, the experiments consisted in first determining the concentration of potassium nitrate, glycerine, urea, and acetamid isotonic with the cell-sap, namely such a solution as would just

*Contribution from the Botanical Department of Cornell University No. 104. Numbers 1–102 are listed in a History of Cornell University, published by The University Publishing Society of New York City, 1905.

produce plasmolysis. When these isotonic concentrations were determined, specimens were placed in the required concentration of glycerine, urea, or acetamid, and left until turgidity was restored. They were then tested with potassium nitrate to determine the concentration necessary to replasmolyze them. The exact method of experiment differed according to the material used, and may best be described under each material.

In order that more accurate results might be obtained, normal solutions of the substances used were made. The solutions were made up on the basis of taking the number of grams represented by the molecular weight of the solute, dissolved in a little distilled water, and this solution diluted to one litre. A normal solution is designated by n, a one half normal by $n/2$, etc.

Philotria

The presence of numerous chloroplasts, as well as the more or less rectangular appearance of the cells in optical section, show incipient plasmolysis readily. The plants used had been in jars of water in the greenhouse for about two months. Fresh sprigs from these were kept in a glass of water, which was frequently changed, on a table near a south window. The importance of having good fresh material cannot be overestimated.

In experimenting with *Philotria*, whole leaves were broken from the stem with a small pair of forceps. This usually injured some of the basal cells, which were therefore not considered in determining the necessary concentration for plasmolysis.

The surplus water was removed from the leaf before applying the plasmolyzing solutions, in order to preserve the concentration of the solution used. Care was taken, however, not to remove too much water, lest the leaf should become flaccid, and vitiate the results. The leaf was mounted in a drop or two of the plasmolyzing solution, under a cover-glass. This solution was drawn off once or twice by filter-paper, and fresh solution added, both to keep the concentration correct and to bring about more rapid diffusion.

Potassium nitrate. Isotonic concentration. — As a result of several general tests, it was found that $n/4$ potassium nitrate would just produce plasmolysis in leaves of *Philotria*. This concentration

did not check cyclosis, and after two hours slow streaming was still visible.

Glycerine. (*a*) *Isotonic concentration.* — $n/3$ glycerine was the concentration required to produce plasmolysis in *Philotria*.

(*b*) *Increase in concentration of cell-sap.* — In order to determine the increase in the concentration (for potassium nitrate) due to the action of glycerine, a few leaves were placed in Van Tieghem cells filled with $n/3$ glycerine. After a lapse of some hours these were tested with solutions of potassium nitrate.

(1) $n/4$ potassium nitrate, the isotonic concentration, did not plasmolyze cells of *Philotria*, which had been in $n/3$ glycerine about five hours.

(2) It required $n/3$ potassium nitrate to plasmolyze cells which had been in $n/3$ glycerine five hours. The action was very uneven, showing complete plasmolysis in some cells and none in others, especially the apical cells. This was no doubt due to the greater permeability of the apical cells, which had therefore absorbed more glycerine.

(3) From $2n/5$ to $9n/20$ potassium nitrate was required to plasmolyze cells which had been in $n/3$ glycerine twenty-four hours.

The above experiments show that not only is the concentration of the cell-sap increased by the penetration of glycerine, but that the longer the action is allowed to go on the stronger the osmotic pressure of the cell-sap becomes.

Urea. (*a*) *Isotonic concentration.* — $n/4$ urea usually failed to plasmolyze cells of *Philotria*, but $n/3$ urea would plasmolyze nearly every cell.

(*b*) *Increase in concentration of cell-sap.* — Leaves were put in solutions in Van Tieghem cells, as in the above experiments with glycerine. Since $n/4$ urea sometimes produced plasmolysis, tests were made for increase in concentration of sap with both $n/4$ and $n/3$ urea.

(1) $n/3$ potassium nitrate produced only incipient plasmolysis in a few cells of leaves which had been in $n/4$ urea about twenty-four hours.

(2) $2n/5$ potassium nitrate was required to produce plasmolysis in such cells. The action was slow and gradual, varying from incipient to strong.

(3) $9n/20$ potassium nitrate was required to produce plasmolysis in leaves which had been in $n/3$ urea about seven hours.

Acetamid. — Since recovery from plasmolysis by acetamid usually occurs in a few minutes, the tests for increase in concentration of the sap were made upon the same cells soon after turgidity was restored.

(1) $n/3$ acetamid showed incipient plasmolysis. The cells were slowly replasmolyzed by $n/3$ potassium nitrate, incipiently at the apex, but stronger toward the base.

(3) $n/2$ acetamid plasmolyzed nearly all cells. It required from $n/3$ to $n/2$ potassium nitrate to replasmolyze such cells.

Tradescantia discolor

Free-hand sections were cut from the lower epidermis of *Tradescantia discolor*, whose cells have a red or violet-colored sap. These were mounted directly in the plasmolyzing solutions. The experiments showed a remarkable variation in the reaction of individual cells of a section, even in the same solution. In some merely incipient plasmolysis was produced, in others the action was quite strong. The cells over a vein were often more easily plasmolyzed than those between the veins.

Potassium nitrate. Isotonic concentration.—From $n/5$ to $n/6$ potassium nitrate was required to produce plasmolysis in *Tradescantia*. The action was more uniform with the $n/5$ solution.

Glycerine. (*a*) *Isotonic concentration.* — From $n/4$ to $n/5$ glycerine was necessary to produce plasmolysis. $n/5$ glycerine plasmolyzed most of the cells incipiently, whereas $n/4$ glycerine plasmolyzed all the cells clearly, some completely.

(*b*) *Increase in concentration of cell-sap.*

(1) In sections which had been in $n/5$ glycerine from six to eight hours, $n/5$ potassium nitrate showed no plasmolysis in most cells, though slight plasmolysis appeared in a few cells.

(2) $n/3$ potassium nitrate produced plasmolysis in such cells.

Urea. (*a*) *Isotonic concentration.* — $n/5$ to $n/6$ urea produced plasmolysis. The degree varied considerably with both solutions.

(*b*) *Increase in concentration of cell-sap.* — Sections of the lower epidermis of *Tradescantia* leaves were put in $n/5$ and in $n/6$ urea, and left seven or eight hours.

(1) $n/4$ potassium nitrate produced plasmolysis in the cells near a vein, but the action was very irregular.

(2) $n/3$ potassium nitrate produced plasmolysis in the cells as a whole.

(3) In sections which had been in $n/6$ urea about eight hours, $n/6$ potassium nitrate produced very slight plasmolysis in a few cells, but $n/5$ potassium nitrate plasmolyzed nearly all the cells, some quite strongly, thus showing that $n/6$ urea was not strong enough to increase the concentration of the sap.

Acetamid.

(1) $n/4$ acetamid was determined as the isotonic concentration. Sections which had been plasmolyzed by $n/4$ acetamid were replasmolyzed by $n/5$ potassium nitrate.

(2) $n/5$ acetamid plasmolyzed some cells, but the action was slow due to the weakness of the solution. $n/5$ potassium nitrate was required to plasmolyze such sections.

Beta vulgaris

Free-hand sections were cut from a red beet and mounted in a drop or two of the plasmolyzing solution, under a cover-glass. The cells near the epidermis were found best to work with, since they were of a deep-red color, and readily showed any change of position of the plasmatic membrane. But the paler parenchyma-cells were also considered.

Potassium nitrate. Isotonic concentration.

(1) $n/2$ potassium nitrate produced slight plasmolysis in some cells of red beet.

(2) $2n/3$ potassium nitrate produced plasmolysis in all cells; plasmolyzed strongly.

Glycerine. (*a*) *Isotonic concentration.* — $2n/3$ glycerine was found to be the isotonic concentration.

(*b*) *Increase in concentration of cell-sap.* — In carrying on experiments to determine the increase in concentration, sections of the beet were placed in small vials holding from 8 to 12 c.c. of solutions used. Turgidity was restored in five or six hours in sections of beet placed in $2n/3$ and also in $n/2$ glycerine.

(1) Cells which had been in $2n/3$ glycerine for six hours were replasmolyzed by $1.6n$ potassium nitrate. A few were replasmolyzed by $1.5n$ potassium nitrate.

(2) Those which had been in $n/2$ glycerine for six hours were replasmolyzed by $1.5n$ potassium nitrate; but the concentration increased later, so that $1.6n$ was required to produce plasmolysis.

The concentration did not exceed this in twenty-four hours.

Urea. (*a*) *Isotonic concentration.* — $3n/2$ urea just plasmolyzed the cells of red beet.

(*b*) *Increase in concentration of cell-sap.* — Sections which had been in $3n/2$ urea for seven hours, were replasmolyzed by $1.6n$ urea.

Acetamid. — $3n/2$ acetamid plasmolyzed these cells in about a minute. The action was a little stronger than with $3n/2$ urea. Turgidity was usually restored in three to ten minutes.

(1) $3n/2$ potassium nitrate plasmolyzed these cells, slowly.

(2) $2n$ potassium nitrate produced too strong a plasmolysis.

(3) n potassium nitrate did not plasmolyze the cells at all.

Spirogyra

Fresh *Spirogyra* was obtained in April, and experiments carried on with this. A few threads were mounted on a slide, under cover-glass, in the plasmolyzing solution, which was drawn off two or three times by filter-paper, and fresh solutions applied. In testing for increase of concentration with glycerine, urea, and acetamid, some *Spirogyra* was put in the required solutions in small vials of about 15 c.c. capacity. In this way plenty of material could be used, and there was a better opportunity for obtaining uninjured threads.

Potassium nitrate. Isotonic concentration. — $n/5$ potassium nitrate usually produced slight plasmolysis, sometimes a stronger plasmolysis. In some cases, however, there was no plasmolysis produced by this concentration.

$n/4.5$ potassium nitrate produced plasmolysis in all cells. The degree varied from slight to rather strong, usually slight.

In these experiments, as in the others, there were usually one or two threads which were more difficult to plasmolyze than the others.

Glycerine. (*a*) *Isotonic concentration.*— $n/4$ glycerine produced incipient to slight plasmolysis in nearly all the cells. $n/3$ glycerine plasmolyzed all the cells.

In most of the cells the plasmolysis was slight, the protoplast withdrawing merely at the corners. In others it was stronger, so that the protoplast separated entirely from the end walls and formed ellipsoidal bodies.

(*b*) *Increase in concentration.*— It required $9n/20$ potassium nitrate to replasmolyze cells which had been in $n/4$ glycerine from four to five hours. $9n/20$ potassium nitrate plasmolyzed only some of the cells which had been in $n/3$ glycerine from four to five hours. $n/2$ potassium nitrate was required to replasmolyze all the cells. It required $2n/3$ potassium nitrate to replasmolyze cells which had been in $n/3$ or $n/4$ glycerine for twenty-four hours.

Urea. (*a*) *Isotonic concentration.* — $n/3$ urea plasmolyzed the cells incipiently or slightly.

$n/2$ urea produced a stronger plasmolysis in all the cells.

(*b*) *Increase in concentration.* — $n/2$ potassium nitrate was required to produced plasmolysis in cells which had been in $n/3$ urea from four to six hours.

$2n/3$ potassium nitrate was necessary to replasmolyze cells which had been in $n/2$ urea for five hours.

Most of the threads were too greatly injured to test the concentration after twenty-four hours.

Acetamid. (*a*) *Isotonic concentration.* — $2n/3$ acetamid seemed to be the isotonic concentration. The plasmolysis varied from incipient to medium strong, and recovery was usually rapid

$n/2$ acetamid produced only very slight plasmolysis in some of the cells.

(*b*) *Increase in concentration.* — It required $2n/3$ potassium nitrate to replasmolyze cells which had been in $2n/3$ acetamid from five to ten minutes.

$n/2$ potassium nitrate produced plasmolysis in cells which had been in $n/2$ acetamid from five to ten minutes.

Acetamid is very injurious in its action on *Spirogyra.* Many threads showed signs of injury in less than two minutes. Only those which seemed healthy and uninjured were considered in the above experiments.

SUMMARY

The results of the above experiments may be summarized in the following tables:

TABLE I

ISOTONIC CONCENTRATION

Plant.	Potassium nitrate.		Glycerine.		Urea.		Acetamid.	
	Normal.	%	Normal.	%	Normal.	%	Normal.	%
Philotria (leaf).	$\frac{1}{4}$	2.52	$\frac{1}{3}$	3.07	$\frac{1}{3}$	2.0	$\frac{1}{2}$–$\frac{1}{3}$	2.95–1.97
Tradescantia discolor (lower epidermis).	$\frac{1}{5}$–$\frac{1}{6}$	2.02–1.68	$\frac{1}{4}$–$\frac{1}{5}$	1.84–1.53	$\frac{1}{5}$–$\frac{1}{6}$	1.2–1.0	$\frac{1}{4}$–$\frac{1}{5}$	1.48–1.18
Beta vulgaris (root).	$\frac{2}{3}$	6.73	$\frac{2}{3}$	6.13	$\frac{2}{3}$	9.0	$\frac{2}{3}$	8.85
Spirogyra.	$\frac{1}{4.5}$	2.25	$\frac{1}{3}$	3.07	$\frac{1}{3}$–$\frac{1}{2}$	2.0–3.0	$\frac{2}{5}$	3.94

TABLE II

INCREASE IN CONCENTRATION OF CELL-SAP

Plant.	Plasmolyzing agent.	Concentration of plasmolyzing agent.		Duration of action.	Isotonic concentration of KNO_3.		Increase of KNO_3.	Increase in concentration of cell-sap.
		N.	%		N.	%	%	
Philotria.	Glycerine.	$\frac{1}{4}$	3.07	5 hrs.	$\frac{1}{4}$	3.36	0.84	1.33
		$\frac{1}{3}$	3.07	24 "	$\frac{9}{20}$	4.55	2.03	1.80
	Urea.	$\frac{1}{4}$	2.0	7 "	$\frac{9}{20}$	4.55	2.03	1.80
		$\frac{1}{5}$	1.5	24 "	$\frac{7}{20}$	4.04	1.52	1.60
	Acetamid.	$\frac{1}{2}$	2.95	15 min.	$\frac{1}{3}$–$\frac{1}{2}$	3.36–5.05	0.84–2.53	1.33–2.0
		$\frac{1}{3}$	1.97		$\frac{1}{3}$	3.36	0.84	1.32
Tradescantia discolor.	Glycerine.	$\frac{1}{4}$	1.84	6 hrs.	$\frac{1}{3}$	3.36	1.34–1.68	1.66–2.0
	Urea.	$\frac{1}{5}$	1.2	7 "	$\frac{1}{5}$	2.02	0–0.34	1–1.2
		$\frac{1}{6}$	1.0	8 "	$\frac{1}{5}$	2.02	0–0.34	1–1.2
	Acetamid.	$\frac{1}{5}$	1.18	30 min.	$\frac{1}{5}$	2.02	0–0.34	1–1.2
		$\frac{1}{4}$	1.48	30 "	$\frac{1}{5}$	2.02	0–0.34	1–1.2
Beta vulgaris.	Glycerine.	$\frac{2}{3}$	6.13	6–24 hrs.	1.6	16.16	9.43	1.4
	Urea.	$\frac{2}{3}$	9.0	7 "	1.6	16.16	9.43	1.4
	Acetamid.	$\frac{2}{3}$	8.85	10–15 min.	$\frac{3}{2}$	15.15	9.42	1.6
Spirogyra.	Glycerine.	$\frac{1}{4}$	1.84	4–5 hrs.	$\frac{9}{20}$	4.55	2.30	2.02
		$\frac{1}{3}$	3.07	4–5 "	$\frac{1}{3}$	5.05	3.30	2.24
		$\frac{1}{4}$, $\frac{1}{3}$		24 "	$\frac{2}{3}$	6.73	4.48	2.99
	Urea.	$\frac{1}{3}$	2.0	4–6 "	$\frac{1}{3}$	5.05	2.80	2.24
		$\frac{1}{2}$	3.0	5 "	$\frac{2}{3}$	6.73	4.48	2.99
	Acetamid.	$\frac{2}{3}$	3.93	5–10 min.	$\frac{2}{3}$	6.73	4.48	2.99
		$\frac{1}{2}$	2.95		$\frac{1}{2}$	5.05	2.80	2.24

DISCUSSION

In carrying on plasmolytic experiments remarkable variability in the reaction of different cells, tissues, and plants may be observed. Yet there seem to be very definite influences at work which affect osmotic activity.

Variation in different plants. — It seems quite evident that plants may adapt themselves to environment in which it is difficult to obtain or to retain water, by increased concentration of the cell-sap. Pantanelli (19) quotes Cavaras to the effect that cold-enduring, salt and rock plants possess a very concentrated cell-sap. Ganong (8) remarks that there seems to be a close correspondence between halophilism of the plant and the power of its root-hairs to resist plasmolysis. The above experiments show that cells of the red beet have a much more concentrated cell-sap than *Tradescantia*.

Variation in different parts of plants. — De Vries (29) notes that the concentration necessary for plasmolysis differs for different parts or tissues of a plant, as well as for different plants. Apical cells have been generally considered to be much more difficult to plasmolyze than other cells, and the limit of concentration necessary to produce plasmolysis to decrease as the age of the cell increases (*cf.* Pfeffer 23, page 317; Ewart 6, page 12; de Vries 29). The above experiments with *Philotria* showed these variations clearly. The cells of the midrib were very difficult to plasmolyze, while those in adjoining parenchyma were usually among the first to show plasmolysis, as well as being plasmolyzed more strongly. But there seems to be some relation between the plasmolyzing substance in the substratum and the reaction of the apical and older cells, which would result from the varying permeability of the protoplast for different substances. In solutions of potassium nitrate and of urea, the cells near the midrib were plasmolyzed to a greater degree than the apical cells. The degree of plasmolysis, incipient in the apical cells gradually, increased in the older cells. With glycerine, however, the stronger plasmolysis occurred in the apical cells. But these cells, after turgidity had been restored, were the last to be replasmolyzed by potassium nitrate. Their greater permeability had allowed more of the glycerine to penetrate the protoplast, so that the concentration of the cell-sap was increased to a greater extent.

Permeability of plasma-membrane. — The permeability of the plasma membrane has been shown for many substances. Hampe (9), Beyer (2), de Vries (33), Klebs (10) and others have shown

that urea and glycerine readily penetrate the protoplast without injury. Klebs (10, page 540) states that glycerine not only penetrates the protoplast, but is there metamorphosed, and as shown by Meyer (14*b*) and Laurent may be converted into starch by certain higher plants; but, he continues, that the presence of glycerine in the cell-sap does not increase the turgor, since water-extraction by potassium nitrate took place normally.

Other experiments do not seem to bear out this view. De Vries found that the osmotic pressure was increased by urea (33*b*) and glycerine (33*a*) so that a much stronger concentration of other plasmolyzing solutions was required to induce plasmolysis again. Famintzin's experiments (7) with the culture of algae showed that by a gradual increase in the concentration of the medium a very considerable number of salts could be transferred into the cell-sap, and the cells in this way accustomed to stronger solutions.

The experiments in the present investigation showed, in nearly every case, an increase in the concentration of the cell-sap under the influence of glycerine, urea, and acetamid. Of the plants used in the experiments, *Tradescantia* showed the least concentration in cell-sap, and the least increase in concentration. Yet in some cases glycerine doubled the concentration of the sap, and the action in general was much stronger than with urea or acetamid. Urea increased the concentration in *Tradescantia* much less than in the other plants studied.

Relation between increase of concentration of sap, and concentration of solution. — There is considerable difference in the action of these substances. Although the final concentrations often do not show great differences, if these concentrations are compared with the original concentrations of the plasmolyzing substances, the greater increase in osmotic pressure due to glycerine will be brought out. The results with red beet cells may be cited as an example. The plasmolyzing concentration of glycerine was $2n/3$, that of urea $3n/2$ which gives a difference of $5n/6$. Yet the same or a less concentration of potassium nitrate was required to replasmolyze cells treated with these solutions, showing that glycerine was able to produce a comparatively greater osmotic pressure than urea.

This difference is much more marked in the case of acetamid.

The concentrations necessary to plasmolyze *Spirogyra* cells were $n/3$ glycerine, and $n/2$ acetamid. But the glycerine produced as great an osmotic pressure as the acetamid.

The action of acetamid in general seems to differ markedly from that of glycerine and urea. The latter substances produce a final concentration in the cell considerably higher than that of the plasmolyzing solution. For example, in the experiments just quoted the $n/3$ glycerine required an $n/2$ potassium nitrate to produce replasmolysis. But acetamid produces a final osmotic pressure equal to that of the solution used to plasmolyze the cells. An $n/2$ acetamid required an $n/2$ potassium nitrate to produce replasmolysis.

The above variations in the increase of concentration tend to show that the time necessary for the recovery of turgidity needs to be considered. After treatment with glycerine or urea, which require several hours for the plant to recover turgidity, a stronger concentration of potassium nitrate is required for replasmolysis, than after treatment with acetamid, in which the plant quickly regains turgidity. This was shown not only in *Philotria* but to a less extent in *Tradescantia*. — In *Philotria* it requires from $9n/20$ to $2n/5$ potassium nitrate to replasmolyze cells which have been plasmolyzed with $n/3$ solutions of glycerine or urea, whereas $n/3$ potassium nitrate produced plasmolysis in cells treated with $n/3$ acetamid. During the hours in which turgidity is being restored in cells plasmolyzed by glycerine or urea, osmotically active products may be formed in the cells. The short time required for turgidity to be restored in acetamid, as well as the fact that turgor is not raised above the osmotic pressure of the plasmolyzing solution, would seem to show that the increased turgor, in this case, was due merely to the penetration of the surrounding solution.

The strength of the solution used also has an influence on the increase of sap-concentration. A more concentrated solution will produce a greater increase in turgor than a weaker solution. The concentration of the sap in *Philotria* was increased 1.8 times in $n/3$ urea, but only 1.6 times in $n/4$ urea; or, expressed in terms of the increase in per cent. of potassium nitrate, 2.03 per cent. in $n/3$ urea, 1.52 per cent. in $n/4$ urea. Acetamid showed a marked difference in *Philotria*. In $n/2$ acetamid the concentration was

doubled, whereas in *n*/3 acetamid the concentration was only 1.33 times the normal sap. That, in general, there is an optimum concentration of the solution which will produce a maximum increase in turgor, and a maximum concentration of the solution beyond which no further increase in turgor will take place, and which may cause the death of the plant, has been shown by the experiments of Starge (26).

CONCLUSIONS

The concentration of cell-sap varies in different plants. It is comparatively weak in *Tradescantia discolor*, but much more concentrated in *Beta vulgaris*.

The limit of concentration necessary to produce plasmolysis varies in different parts and tissues of the plant according to the age of the cell, to the permeability of the protoplast, and to the plasmolyzing substance. With potassium nitrate and urea, the apical cells of *Philotria* were plasmolyzed incipiently, and the degree of plasmolysis gradually increased in the older cells. Glycerine, however, produced strongest plasmolysis in the apical cells. In all cases a stronger concentration of glycerine than of potassium nitrate was required to produce plasmolysis. Acetamid required the strongest concentration of the solutions used. The concentration of urea varied, but was sometimes stronger than that of glycerine.

The concentration of the cell-sap may be increased by the penetration of glycerine, urea, or acetamid. A comparison of the increase in concentration due to the various substances shows that glycerine produces relatively, and sometimes actually, the greatest increase. For, although, in some cases, as in *Philotria* and *Spirogyra*, urea and acetamid may produce a greater actual increase, this was due to the greater concentration of the plasmolyzing solutions. Acetamid cannot increase the concentration of the sap above the concentration of the plasmolyzing solution.

The duration of the action of the plasmolyzing solution influences the increase in the concentration of the sap. Glycerine and urea, whose action continues several hours, produce a relatively greater increase in the concentration than acetamid, whose action is very quick. The increase in the concentration of the sap of *Spirogyra* in solutions of glycerine was greater after twenty-four hours than after five hours.

The concentration of the plasmolyzing solution influences the increase in the concentration of sap. *n*/2 urea increased the concentration of sap in *Spirogyra* 2.99 times, whereas *n*/3 urea increased it 2.24 times. The greater increase takes place in the stronger concentration of the plasmolyzing solution.

This paper was submitted by Professor Atkinson to Professor Wilder D. Bancroft of the Chemical Department, who very kindly read it for the purpose of passing on the question of chemistry involved. He has suggested that the increase in concentration is due to the fact that the solutions, glycerine, urea, and acetamid pass through the plasma-membrane into the cell-sap, until the concentration of the solutes used is equal on both sides of the membrane, without reference to the concentration of other substances in the sap. Thus the total concentration in the sap may be equal to the original concentration of the sap plus the concentration of the glycerine, urea, or acetamid solutions used. Turgor would be restored when enough of the solution had penetrated so that the total concentration within the cell equaled the concentration in the external medium. If the plant remained in the solution after the turgor was restored, osmotic action might continue until the concentration of the solutes used would be equal on both sides of the membrane, and the total concentration would be greater than that of the external solution.

This hypothesis would explain the cases where the increase in concentration was equal to or less than the concentration of the plasmolyzing solution, as in the experiments with *Tradescantia* and *Philotria*, and all the experiments with acetamid. The increase in concentration above that of the external solution, amounting in *Beta* to 6.88 per cent., and in *Spirogyra* from 1.33–1.48 per cent. in glycerine solution, seems remarkable. In this connection reference may be made to the conclusion of Loeb (Studies in General Physiology, page 553) that "the simple osmotic theory of absorption which has been accepted by botanists cannot possibly be correct." This conclusion was based upon experiments with muscles, and *Fundulus*. "The fact that *Fundulus* can be thrown from sea-water into distilled water without any considerable swelling, or without any visible injurious effects, may find its explanation through the influence that various ions have upon the absorption of liquids."

Further investigations are needed to determine the causes for such an increase in concentration. Whether the substances undergo changes within the cell, and to what extent the changes take place, might be revealed in experiments upon growth of plants in the different solutions.

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Chroolepus aureus a lichen

ALBERT SCHNEIDER

(WITH PLATE 22)

During my study of the lichen formations in the vicinity of the Minnesota Seaside Station (near Port Renfrew, Vancouver Island, B. C.), I frequently found *Chroolepus aureus* (L.) Kütz. [*Trentepohlia aurea* (L.) Mart.] on trees (spruce and hemlock) and on rocky ledges overhanging the beach. It is exceedingly abundant in certain circumscribed areas and shows great variability in the length of filaments. There was also observable a marked difference in color, varying largely between that of old gold and a bright orange-brown. As to whether the difference in color indicated two distinct species I will not venture an opinion at present, although the indications are that that is the case. It is very essential that these plants should be studied in the fresh state as they lose the characteristic color very quickly when placed in the herbarium, which increases the difficulties in the way of identification.

The representatives of the genus *Chroolepus* are especially interesting because of their tendency to associate themselves biologically with fungi to form lichens. *Chroolepus umbrinus* (represented in thirteen lichen genera), or a species closely similar to it, forms the algal symbiont of many lichen species. Bearing this in mind, a more careful study was made of *C. aureus*, to determine if this plant presented this character to any marked degree. Fresh material, obtained from ledges of overhanging sandstone and from trunks and branches of hemlocks, was carefully examined under the microscope. The normal filaments showed a variation in length as shown in PLATE 22. The cells contain numerous reddish-brown granules or globules. Very frequently there was found a twining hyphal fungus, especially abundant about the bases of the filaments. This fungus was, however, not sufficiently constant in its appearance to warrant the assumption that it represented a marked biological association with the alga, either antagonistic or mutualistic. More likely it represents merely an accidental association, due to the fact that both organisms live upon the same

substratum and require the same or similar moisture and light conditions.

The interesting feature, however, was a delicately reticulate, spirally wound, network of what appeared to be the hyphal tissue of a fungus which entirely enwrapped the algal threads from base to apex and projected a short distance beyond the apex of most threads. In some instances, this structure extended only to the apex or within a short distance of the tip. This network is very firmly attached to the algal cell-wall. Only after the application of strongly alkaline or strongly acid solutions was it possible to induce it to separate from the algal cells, assisted by pressing the material quite forcibly under the cover-glass. Even then, only fragments could be removed which showed the reticulation very clearly (see plate). The network gives to the filaments a roughened appearance, with here and there a delicate thread (simple or sparingly branched) of the network projecting out from the algal filament. As stated, this mesh-work extends a short distance beyond the apex of the algal thread, in the form of a tube, partially divided across by the same network, thus giving the semblance of partial septation. One, two, or three of these compartments were noticeable, never more. It appears that the compartments are occupied by the new algal cells as the filament grows in length; however, new mesh compartments are always formed in advance of the algal cells.

It would appear that this finely reticulate, colorless network is the hyphal tissue of a fungus which invests the algal filaments, indicating a very intimate biological relationship. It represents a condition not unlike that which exists in the well-known lichen *Ephebe pubescens* Fr., only the fungal symbiont does not penetrate the algal tissue. The hyphal structure of the fungal symbiont in both is closely similar excepting that the anastomoses are much more common in *Chroolepus aureus*. No experiments have been made to determine the biological relationship of the two symbionts, whether antagonistic or mutualistic. Nor was it possible, at the time, to determine conclusively whether or not the fungal symbiont is always present. It was present in all of the material examined, although specimens were found in which the reticulation was rather indistinct. Some authors speak of this terminal

structure as a "cellulose cap," without explaining its nature and use.

There seems to be little doubt that the network described represents a fungus symbiotically associated with the alga *Chroolepus aureus*. This association appears to be sufficiently constant to warrant placing this structure, heretofore classed as an alga, with the class *Lichenes*. The fungal symbiont does not appear to develop spores or any of the other special structures found with the fungal symbionts of the majority of lichens.

UNIVERSITY OF CALIFORNIA, DEPARTMENT OF PHARMACY.

Explanation of plate 22

A, Filaments of *Chroolepus aureus*, showing the enclosing fungal meshwork (a, b) and special algal filaments (c).

B, Long filaments of *Chroolepus* with the enclosing meshwork removed.

C, Terminal portion of algal filament, more highly magnified. The extreme tip is always free of the fungal symbiont.

D, Basal portion of algal filament, showing the delicate meshwork (b) and the twining filaments of a coarser hyphal fungus (a).

E, A portion of the fungal meshwork removed from the algal filament, showing the characteristic reticulation.

Magnification of *A* and *B* about 225 diameters, of *C*, *D* and *E* about 300 diameters.

Poa gracillima Vasey and its allies

CHARLES VANCOUVER PIPER

The *Poa* species of the group related to *P. gracillima* Vasey are separable with difficulty, and distinguished only by slight characters. They are characterized among the western poas by their tufted habit, narrow flaccid leaves, loose open panicles, and by their growing on cliffs. The 7 species may be distinguished by the following key:

Ligules of the sterile shoots obsolete or nearly so, those of the culm-leaves short and truncate. *P. Multnomae.*

Ligules of all the leaves moderately developed, 1–2 mm. long.

Low plants, 5–10 cm. high; panicle small, usually purple, of few spikelets, the rays divaricate. *P. vaseyochloa.*

Taller, 10–30 cm. high; panicle with many spikelets, the rays not divaricate.

Panicle rather close; spikelets 6–9 mm. long; glumes of firm texture; blades flat. *P. saxatilis.*

Panicle loose; spikelets 7 mm. long; glumes thin; blades involute. *P. gracillima.*

Ligules of all the leaves rather long, 2–5 mm. long.

Panicle rather stiff, the rays short; blades flat.

Rays in about eight series of 3–5 each; flowering glumes pubescent toward the base. *P. invaginata.*

Rays in about five series of 1 or 2 each; flowering glumes minutely scabrous to the tip, puberulent at base. *P. acutiglumis.*

Panicle loose, the rays somewhat drooping, in about five series of 2 or 3 each; flowering glumes puberulent at base. *P. alcea.*

It is very doubtful if all these species can be maintained. Only careful field work and good series of specimens will enable the problem to be solved. *Poa vaseyochloa* is probably only a starved form of *P. gracillima*, from which *P. saxatilis* also is scarcely distinguishable. The ligule character may prove illusory, but large series of *Poa alcea* and *P. Multnomae* indicate otherwise.

Poa Multnomae sp. nov.

Sporobolus Bolanderi Vasey, Bot. Gaz. **11**: 337. 1886. Not *Poa Bolanderi* Vasey, Bot. Gaz. **7**: 32. 1882.

Perennial, densely tufted, with numerous slender innovations: culms slender, 2- or 3-jointed, often geniculate at base, terete,

smooth, and shining, 10–30 cm. high: sheaths glabrous, faintly striate, often purplish, shorter than the internodes; blades narrow, soft, smooth, folded or sometimes flat, 8–12 cm. long; ligules scarious, those of the culm 1–2 mm. long, of the innovations nearly obsolete: panicle loose, often one-sided, 5–10 cm. long, usually pale-green, sometime purplish, the slender, nearly smooth rays in about five series of 2 or 3 each: spikelets broadly lanceolate, 5–7 mm. long, 3–5-flowered: empty glumes lanceolate, smooth, scarious-margined, 3-nerved, the lower about 3 mm., the upper 4 mm. long; flowering glume ovate, acutish, sparsely crisp-puberulent at base, the lateral nerves disappearing in the scarious apex; palet as long as the flowering glume, notched at apex, the nerves ciliate-scabrous.

Type specimens collected at Multnomah Falls, Oregon, June 25, 1904, *Piper 6459*. This is the common *Poa* on the cliffs along the Columbia River, heretofore confused with *P. gracillima* Vasey.

The type of *Sporobolus Bolanderi* Vasey is also from Multnomah Falls, and is an overmature specimen from which most of the spikelets have fallen, which led to its being mistaken for a *Sporobolus*. On account of its poor condition, I indicate a new type for the species.

Poa alcea sp. nov.

Perennial, tufted, with numerous innovations: culms slender, terete, erect, smooth, 2- or 3-jointed, 30–50 cm. high: sheaths smooth, shorter than the internodes, often purplish; blades soft and smooth, narrowly linear, folded or loosely involute, 8–15 cm. long; ligules scarious, ovate, decurrent, those of the culm-leaves 2–4 mm. long, of the basal leaves shorter: panicle lax, pyramidal, often somewhat drooping, 5–12 cm. long; rays in about 5 series, mostly in twos and threes, and unequal, sparsely scabrous: spikelets oblong, 6–9 mm. long, mostly 5-flowered, pale-green or somewhat purple-tinged: empty glumes smooth, scarious-margined, oblong-lanceolate, acutish, the lower 1-nerved or sometimes 3-nerved, 3 mm. long, the upper longer, somewhat broader, 3-nerved; flowering glume thin-membranous, elliptic-ovate, obtuse, 3.5–4 mm. long, silvery-puberulent near the base, the lateral nerves vanishing in the scarious apex; palet oblong, notched at apex, as long as the flowering glume, the nerves ciliate-scabrous, the lateral portion half as broad as the internerve.

Abundant on Elk Rock near Portland, Oregon, where it was collected June 3, 1904, *Piper, 6463*. The following specimens also are referred here, all of Oregon:

Trask River, *Howell 761* in 1880; without locality, *Howell 73*, July 11, 1882, and *Henderson 9*, in 1883.

This is certainly exceedingly close to *Poa Multnomae* described above, but the ligule character, which seems very constant in the difficult western poas, together with the larger size, is relied upon to distinguish it.

From *Poa acutiglumis* Scribn. it may be distinguished by its more lax, larger panicles, larger leaves, smaller spikelets, and different flowering glumes.

BUREAU OF PLANT INDUSTRY,
UNITED STATES DEPARTMENT OF AGRICULTURE.

INDEX TO AMERICAN BOTANICAL LITERATURE

(1905)

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in its broadest sense.

Reviews, and papers which relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omission their kindness will be appreciated.

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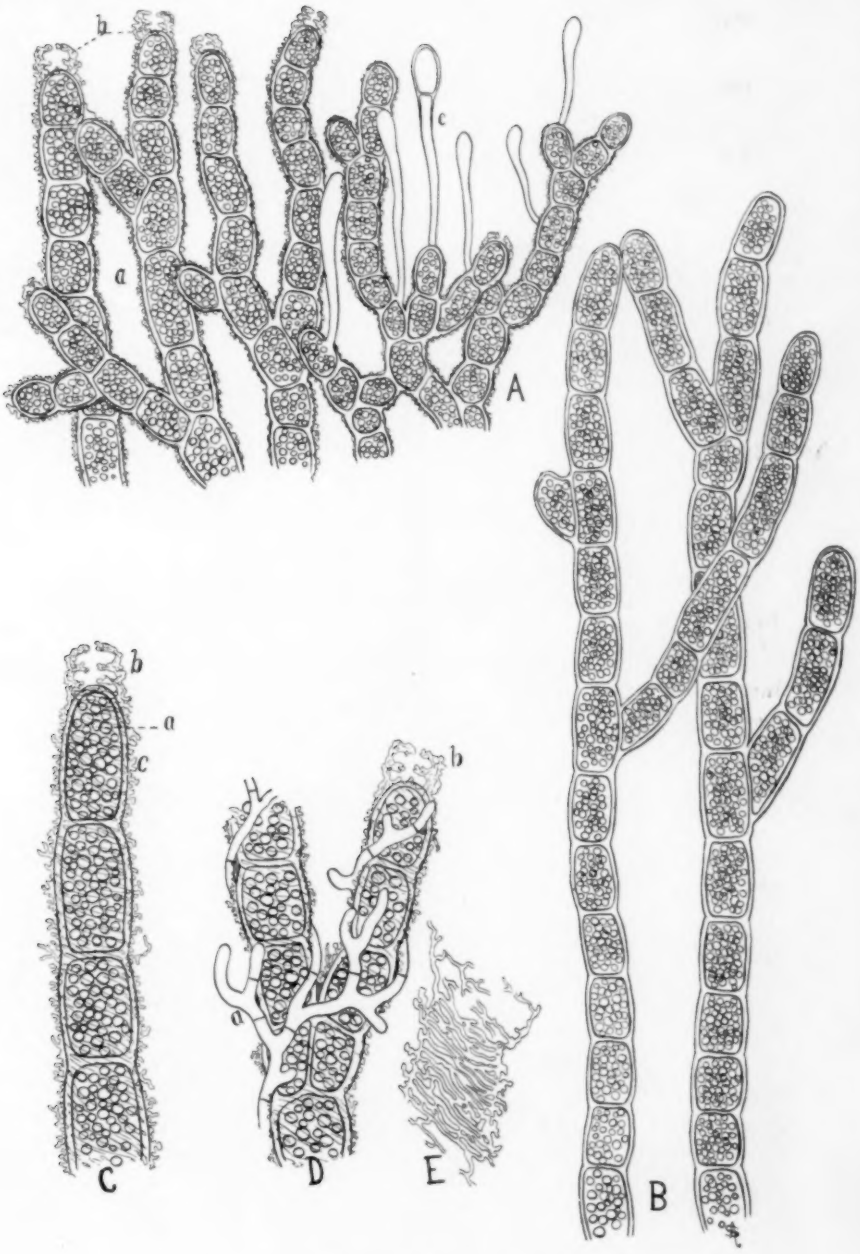

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